



The cost of avoiding predators: a bioenergetic analysis of diel vertical migration by the opossum shrimp *Mysis diluviana*

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Abstract The freshwater opossum shrimp *Mysis diluviana* can undergo extensive diel vertical migration (DVM) to feed in shallow, prey rich strata at night. Bright moonlight limits their nighttime migration presumably due to predator avoidance. Using a linked, foraging-bioenergetics model, we evaluated the cost of avoiding predators by simulating the effects of prey density, water temperature, and light intensity on daily feeding and growth of *M. diluviana* in Lake Pend Oreille, Idaho, USA. We found that when mysid distribution was not limited

by moonlight intensity, simulated food consumption (10.3 J day^{-1}) increased 1.6-fold compared to estimated consumption (6.1 J day^{-1}) based on their observed, vertical distribution. Moreover, simulated growth of mysids (0.61 mg day^{-1}) increased 74% compared to that estimated from observed distribution patterns (0.35 mg day^{-1}), when they were located in deeper, darker strata. Given recent insights into partial DVM by *M. diluviana*, we note that proximate factors associated with predator avoidance in pelagic (light availability) and benthic (hunger level, body size and reproductive status) habitats may convey complimentary benefits to *M. diluviana* fitness by reducing predation mortality and increasing metabolic efficiency.

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Introduction

Fish predation is a strong, selective force in shaping diel vertical migration (DVM) behavior in zooplankton (Gliwicz, 1986). The freshwater opossum shrimp *Mysis diluviana* Audzinytė & Väinölä, 2005 is a widely distributed invertebrate predator in North American lakes that undergoes extensive DVM, often ascending from daytime depths greater than 300 m to forage on phytoplankton and zooplankton at night (Beeton, 1957). Relative changes in light intensity are

a proximate cue in initiating and controlling DVM by *M. diluviana* (Teraguchi et al., 1975) although other factors such as water temperature (Mauchline, 1980; Rudstam et al., 1999; Chipps & Bennett, 2000) and food availability (Gal et al., 2004) can influence the extent and magnitude of their daily migrations.

Due to the relatively large size of *M. diluviana* (up to 2 cm), avoidance of visually feeding fishes is believed to play an important role in shaping their DVM behavior (Gal et al., 2004; Boscarino et al., 2010a). Although several hypotheses have been proposed to explain the adaptive significance of DVM by zooplankton (Lampert, 1989; Hays, 2003; Cohen & Forward, 2009), the predator avoidance hypothesis is particularly attractive for *M. diluviana* for several reasons: (i) smaller, and presumably less susceptible mysids begin their daily ascent earlier than larger individuals and migrate higher in the water column where light intensity is greater (Boscarino et al., 2010b), and are the last to descend in early morning (Beeton & Bowers, 1982; De Robertis, 2002), (ii) moonlight intensity is known to disrupt the extent of their nocturnal distribution patterns (Janssen & Brandt, 1980) and, (iii) *M. diluviana* avoids depths with increased levels of kairomones released by fish predators (Boscarino et al., 2007).

Because of their preference for low light levels (Boscarino et al., 2009a, 2010b), the vertical distribution of *M. diluviana* is often constrained on nights with bright moonlight, when they are distributed at deeper, cooler water depths where prey densities are generally low (Janssen & Brandt, 1980). This behavior is particularly notable in late summer (e.g., August) when lakes are thermally stratified and *M. diluviana* feed at night on preferred, pelagic zooplankton (Johannsson et al., 2001). Light-dependent changes in DVM behavior led Beeton & Bowers (1982) to postulate that *M. diluviana* suffer an energetic tradeoff during periods of bright moonlight, a consequence of balancing the risk of predation against greater food consumption (Jensen et al., 2006). Evidence that individuals suffer such an energetic tradeoff would support the hypothesis that the extent of vertical migration in this species has evolved in direct response to predation intensity.

Bioenergetics modeling provides a robust approach for evaluating effects of migration behavior on growth dynamics in aquatic animals (Swift, 1976). The DVM behavior of Kokanee Salmon *Oncorhynchus nerka*

(Walbaum, 1792) was best explained by growth maximization, whereby fish feed in areas where net energy intake is maximized (e.g., shallow, prey rich habitat) and then reside in areas (e.g., deep, cooler habitat) where metabolic costs are minimized (Bevelhimer & Adams, 1993). Bioenergetics modeling of Roach *Rutilus rutilus* (Linnaeus, 1758) populations showed that migrating between lake and stream habitats was an adaptive behavior that minimized the ratio between predation mortality and growth rate (Brönmark et al., 2008).

To explore the impact imposed by bright moonlight on energy acquisition by *M. diluviana*, we estimated nocturnal feeding rates of vertically migrating mysids during dark and bright moon light conditions in Lake Pend Oreille, Idaho, USA. Information on mysid distribution, feeding rate, and thermal history was then combined with a bioenergetics model to estimate daily growth of an adult, migrating mysid (≥ 15 mm). We tested the hypothesis that *M. diluviana* growth is constrained during bright moon conditions by comparing daily growth based on their actual, vertical distribution to that derived from a simulated, vertical distribution where they were assumed to forage in the upper water column at warmer water temperatures and greater light levels.

Methods

Study area

Lake Pend Oreille is a temperate, oligotrophic lake located in the panhandle of northern Idaho, USA. The lake has a surface area of 38,300 ha, a mean depth of 164 m and a maximum depth of 357 m. Thermal stratification usually occurs between July and September with metalimnetic water temperatures averaging 9°C, while surface temperatures rarely exceed 23°C (Rieman, 1976; Chipps & Bennett, 2000). Water levels are controlled by the Albeni Falls Dam and are maintained at an average of 628.7 m above sea level during the summer. The lake contains a variety of fishes, many of them introduced either intentionally for sportfish recreation, or unintentionally via illegal or accidental stockings.

Important pelagic predators of *M. diluviana* include Cutthroat Trout *Oncorhynchus clarki* (Richardson, 1836), Rainbow Trout *Oncorhynchus mykiss*

(Walbaum, 1792) and Kokanee Salmon (Vidregar, 2000). Young Lake Trout *Salvelinus namaycush* (Walbaum, 1792) are also important mysid predators, although during our study the Lake Trout population in Lake Pend Oreille was in the early stages of development. Lake Trout were first documented in the lake in the early 1990s; by 1999, the population was estimated at 1,792 fish or about 0.1 kg Lake Trout ha⁻¹ (Vidregar, 2000). Studies have shown that the Lake Trout population expanded exponentially in Lake Pend Oreille during the early 2000s (Hansen et al., 2008; Dux et al., 2019). Efforts to suppress the Lake Trout population from 2006 to 2016 have been successful in reducing their abundance with >193,000 fish removed by gillnetting, angling and trap netting (Dux et al., 2019). Slimy Sculpin *Cottus cognatus* Richardson, 1836 can also be an important benthic predator of *M. diluviana* (Owens & Weber, 1995), although diets of Slimy Sculpin collected from Lake Pend Oreille contained mostly insects (72%) and small crustacea (26%; Vidregar, 2000).

M. diluviana was introduced annually into Lake Pend Oreille (50,000–300,000/year) from 1966 through 1970 from specimens collected from Waterton Lake, Alberta and Kootenay Lake, British Columbia (Rieman & Falter, 1981). After establishment of the mysid population, the seasonal availability and abundance of Cladocera zooplankton declined in Lake Pend Oreille (Rieman & Falter, 1981). Reduced zooplankton density was later linked to declines in the Kokanee population, the primary planktivorous fish in the lake (Spencer et al., 1991; Chipps & Bennett, 2000; Caldwell et al., 2016). Because *M. diluviana* can be important prey for young Lake Trout (<450 mm), they also likely contributed to the expanding Lake Trout population in the early 2000s (Hansen et al., 2008).

M. diluviana distribution and abundance

Sampling for mysids was conducted at a single, fixed station (47°58'30.39" N 116°31'16.77" W) in the southern basin of Lake Pend Oreille (water depth=213 m). Vertical distribution of mysids was monitored at 30 min intervals between 1900 and 0700 h during a dark (August 16–17th, 1996) and bright (August 26–27th, 1996) moon phase using hydroacoustics (Lowrance X16 200 kHz echosounder, 8° beam width). The upper and lower

boundary of the ascending mysid layer was determined from echosounder output and revealed that *M. diluviana* completed their nighttime ascent by 2,200 h with the lower boundary occurring at depths to 30 m below the water surface.

Because age-0 *M. diluviana* (≤10 mm) are primarily herbivorous until October (Chipps & Bennett 2000), we quantified the abundance (no. m⁻²) and mean size of migrating, adult mysids (≥15 mm) collected using a vertical tow net (0.5 m diameter net; 1,000 μm mesh size) on each night between 2200 and 2300 h. Three to five vertical tows, hauled at a rate of 0.3–0.4 m s⁻¹, were taken from 0 to 9 m, 0 to 18 m, and 0 to 30 m (Chipps & Bennett, 1996). All mysids collected were preserved in 8% formalin and transported to the laboratory where they were measured for total length to the nearest 0.5 mm from the rostrum to the tip of the telson. The average number of adult mysids collected at different depths (e.g., 9 to 18 m) was calculated by subtraction.

Echogram recordings were used to assess: (1) the hourly vertical depth distribution of *M. diluviana*, (2) the time spent feeding in the metalimnion, and (3) the ascent and descent rate associated with DVM. Water temperature (°C) experienced by migrating mysids was determined from nightly temperature profiles measured at 1-m intervals ranging from 1 to 50 m below the surface.

Light levels

Depth-specific light intensity (I_z) in Lake Pend Oreille was calculated as,

$$I_z = I_0 e^{-EZ}, \quad (1)$$

where I_0 is [surface] moonlight intensity (lx), Z is water depth (m), and E is the light extinction coefficient. To estimate I_0 , we used information on the moon phase, time of day, latitude, and longitude as inputs in the model developed by Janiczek & De Young (1987). Light extinction (E) was estimated using an empirical model developed by Scheffer (1998),

$$E = 0.016(\text{Chl}) + \frac{1.3}{\sqrt{S}}, \quad (2)$$

where Chl represents mean August chlorophyll *a* concentration in Lake Pend Oreille (0.0029 mg l⁻¹) and

S represents observed Secchi depth (8 m; Chipps, 1997). We scaled estimated light level I_z to account for the spectral sensitivity of *M. diluviana* by converting lx to mylux; for moonlight, 1 mylux = 175 lx (Gal et al., 1999). Because night-time distribution of *M. diluviana* from field studies and laboratory experiments indicated that they avoid light levels greater than 10^{-6} mylux (Boscarino et al., 2009a, b), we used the water depth at this light intensity as a reference depth to explore effects of moonlight on the upper distribution of the mysid layer. On the 16–17th of August, 2 days after the new moon, overcast skies combined with the dark phase of the moon, made this night particularly dark (4% moon illuminance). Bright moon conditions associated with the full moon phase were best captured during clear skies on August 26–27th (97% moon illuminance).

Prey abundance

Crustacean zooplankton were collected concurrently with *M. diluviana*. To characterize the vertical distribution of crustacean zooplankton, three replicate samples were obtained using a 10 l Schindler trap at depths of 1, 5, 10, 15, 20, 25 and 30 m below the water surface. All crustacean zooplankton were preserved in sugared, 4% formalin (Haney & Hall, 1973). In the laboratory, zooplankton were passed through a series of five sieves (ranging from 1 to 0.1 mm); zooplankton collected in each size fraction were identified to species and enumerated. Twenty individuals per species in each size fraction were randomly selected and measured to the nearest 0.03 mm under

×45 magnification using an ocular micrometer. Individual dry weight (μg) of crustacean zooplankton was determined from length-dry weight regressions and converted to wet weight (g) using a dry:wet ratio of 0.10 (Rieman & Falter, 1981).

Foraging model

We used a linked, foraging-bioenergetics model to estimate daily energy gain by an average, migrating adult *M. diluviana* ≥ 15 mm (Bevelhimer & Adams, 1993). Daily zooplankton consumption by mysids (C , mg prey mysid $^{-1}$ day $^{-1}$) was estimated for six prey types as,

$$C = \sum_{i=1}^6 (CR_i \cdot PD_i \cdot PW_i \cdot H), \quad (3)$$

where CR_i is *M. diluviana* clearance rate for prey $_i$ (1 mysid $^{-1}$ h $^{-1}$; see Table 1), PD_i is depth-specific density of prey $_i$ (no. prey $_i$ l $^{-1}$), PW_i is the mean wet weight of prey $_i$ (mg wet wt), and H are hours spent foraging by *M. diluviana* in the water column (Johannsson et al., 1994). The major assumption in using this model to estimate hourly consumption is that clearance rate and prey density are independent. Although this is a reasonable assumption at prey densities < 25 l $^{-1}$ (Bowers & Vanderploeg, 1982; Nero & Sprules, 1986), at sufficiently high prey densities clearance rate will overestimate hourly food consumption. To evaluate the influence of prey density on hourly food intake, we compared field consumption estimates from Eq. 3 to laboratory-derived

Table 1 Clearance rate by *M. diluviana* for zooplankton taxa collected in Lake Pend Oreille, Idaho, August, 1996

| Order | Species | Life stage | Length-dry weight relationship | <i>M. diluviana</i> clearance rate (L mysid $^{-1}$ h $^{-1}$) |
|--------------------------|---------------------------------|------------|--------------------------------|---|
| Calanoida ^a | <i>Leptodiatomus ashlandi</i> | Adult | 3.47L ^{2.26} | 0.047 |
| | | Copepodid | | 0.193 |
| Cyclopoida ^a | <i>Diaacyclops bicuspidatus</i> | Adult | 7.82L ^{2.55} | 0.237 |
| | | Copepodid | | 0.138 |
| Diplostraca ^b | <i>Daphnia galeata</i> | All | 5.48L ^{2.2} | 0.56 |
| | <i>Diaphanosoma birgei</i> | All | 3.76L ^{2.1} | 0.56 |

Note that clearance rate varies by life stage for Calanoida and Cyclopoida taxa, resulting in the six prey types used in Eq. 3. Length-dry weight relationships are provided for each species where dry weight (DW, μg) is estimated from body length (L, mm)

^aNero & Sprules (1986)

^bBowers & Vanderploeg (1982)

estimates of maximum food consumption for *M. diluviana* using the equation,

$$C_{\max} = 0.0015W^{0.628} \cdot f(T) \cdot H \cdot 1000, \quad (4)$$

where C_{\max} represents maximum feeding rate (mg prey $\text{mysid}^{-1} \text{ day}^{-1}$), W is average body weight of a migrating adult *M. diluviana* ≥ 15 mm ($\bar{x}=0.03$ g, $\text{SE}=0.002$) and $f(T)$ is a temperature-dependent function (Rudstam et al., 1999; Table 2). For modeling simulations, we used estimates of C (Eq. 3) when C/C_{\max} was < 1 ; otherwise, we used C_{\max} (Eq. 4) as input in the bioenergetics model to simulate growth (see below).

Bioenergetics model

Daily growth rate of an average, migrating adult *M. diluviana* was simulated using Fish Bioenergetics 4.0 (Deslauriers et al., 2017). The model represents a mass-balance equation,

$$G = C - (R + \text{SDA} + F + U), \quad (5)$$

where growth (G) is balanced by the energy consumed (C) minus respiratory demands (R and SDA) and waste losses (F and U ; Rudstam, 1989; Chipps, 1998; Chipps & Bennett, 2002). Here, R equals routine metabolism, SDA is specific dynamic action, and F and U are losses due to egestion and excretion,

Table 2 Equations and parameter values used in the combined *M. diluviana* foraging-bioenergetics model

| Symbol | Description | Value |
|---|--|--------------------|
| <i>Consumption, C (Eq. 3)</i> | | |
| CR_i | Clearance rate of prey _{<i>i</i>} ($l \cdot \text{mysid}^{-1} \cdot h^{-1}$) | 0.047–0.560 |
| PD_i | Mean density of prey _{<i>i</i>} (no. prey $\cdot l^{-1}$) | 0.03–43.7 |
| PM_i | Mean mass of prey _{<i>i</i>} (μg wet weight) | 8–160 |
| FT | Time spent foraging in the metalimnion (h) | 6.5–7 |
| <i>Bioenergetics</i> | | |
| <i>Maximum consumption^a, C_{max} (Eq. 4)</i> | | |
| $CK1$ | Proportion of C_{\max} at low temperature (CQ) | 0.85 |
| $CK4$ | Proportion of C_{\max} at high temperature (CTL) | 0.26 |
| CQ | Low water temperature where consumption is a fraction ($CK1$) of the maximum rate (C_{\max}) | 4 |
| CTO | Water temperature ($< CTM$) corresponding to $0.98 C_{\max}$ | 8 |
| CTM | Water temperature ($> CTO$) corresponding to $0.98 C_{\max}$ | 13 |
| CTL | Water temperature at which consumption is some small fraction ($CK4$) of C_{\max} | 20 |
| <i>Metabolism^b, R (Eq. 6)</i> | | |
| F | Proportion of non-assimilated energy that is egested | $0.15 \cdot C$ |
| U | Proportion of assimilated energy that is excreted | $0.18 \cdot (C-F)$ |
| SDA | Proportion of assimilated energy lost to specific dynamic action | $0.18 \cdot (C-F)$ |
| <i>Temperature rate multiplier^c, $f(T) = K_A \cdot K_B$</i> | | Fitted parameter |
| K_A | $(CK1 \cdot L1)/(1 + CK1 \cdot (L1-1))$ | |
| K_B | $(CK4 \cdot L2)/(1 + CK4 \cdot (L2-1))$ | |
| $L1$ | $e^{(G1 \cdot (T-CQ))}$ | |
| $L2$ | $e^{(G2 \cdot (CTL-T))}$ | |
| $G1$ | $(1/(CTO-CQ)) \cdot \ln((0.98 \cdot (1-CK1))/(CK1 \cdot 0.02))$ | |
| $G2$ | $(1/(CTL-CTM)) \cdot \ln((0.98 \cdot (1-CK4))/(CK4 \cdot 0.02))$ | |

All variables are defined except for T , which is water temperature ($^{\circ}\text{C}$). Details of the bioenergetic model are described in Deslauriers et al. (2017)

^aRudstam et al. (1999)

^bRudstam (1989)

^cThornton & Lessem (1978)

respectively. Routine metabolism is modeled as a function of body mass and water temperature whereas other parameters are defined as a constant proportion of consumed energy (i.e., SDA, F, and U; Table 2). For *M. diluviana*, activity-dependent metabolism is considered negligible under normal swimming speeds associated with daily migrations and is captured in measures of routine metabolism (Foulds & Roff, 1976; Rudstam, 1989; Chipps & Bennett, 2002). The model is structured after the popular Wisconsin bioenergetics model (Kitchell et al., 1977) that uses energy density values of predator and prey, along with an oxycaloric adjustment, to standardize all parameter estimates to specific rates in $\text{J J}^{-1} \text{day}^{-1}$ (Deslauriers et al., 2017).

A unique aspect of the model used here, is that growth estimates are based on hourly rather than daily time steps. To account for hourly variation in water temperatures experienced by mysids during migration, routine metabolic rate (R) was expressed as,

$$R(\text{g O}_2 \text{ g}^{-1} \text{ h}^{-1}) = 0.0000758 W^{-0.161} e^{0.0752T} \quad (6)$$

where W is mysid wet weight in g and T is water temperature in $^{\circ}\text{C}$ (Rudstam, 1989).

Other input variables required for the model include predator and prey energy density, hourly water temperature, and daily prey consumption (g wet weight). An energy density value of 3556 J g^{-1} wet weight was used for adult *M. diluviana* ($\geq 15 \text{ mm}$; Lasenby, 1971) while energy density values of 2259 or 2380 J g^{-1} wet wt $^{-1}$ were assigned to cladoceran or copepod prey, respectively (Chipps & Bennett, 2000).

Model simulations

Vertical profiles of prey density were used to estimate hourly feeding rate of an average migrating, adult mysid (wet weight = 30 mg) during nights with dark or bright moonlight. On each night, feeding was assumed to begin when mysids had completed their daily ascent into the metalimnion, and to terminate at the onset of their morning descent. Although mysids likely capture some prey during their ascent and descent through the metalimnion, the relative amount of time spent migrating through this layer is low ($< 0.5 \text{ h day}^{-1}$) compared to the total time spent foraging at night ($> 6 \text{ h day}^{-1}$; Chipps, 1997). For modeling purposes,

daily growth estimates were based on the amount of energy acquired during nocturnal foraging in the metalimnion.

Our primary interest in modeling growth dynamics was to evaluate the potential, energetic tradeoff that *M. diluviana* experience during a bright moon when they are distributed deeper in the water column. To accomplish this, we simulated adult mysid growth during bright moon conditions by assuming they foraged at the warmer water temperatures and shallower water depths observed during the dark moon phase on August 16–17th. Conversely, we simulated daily growth of an adult mysid during the dark moon phase by adjusting their vertical distribution in the water column to match the cooler water temperatures and deeper water depths observed for mysids during the bright moon phase. An overview of the foraging model and the relationships between *M. diluviana* migratory behavior (vertical distribution) and abiotic/biotic conditions are illustrated in Fig. 1.

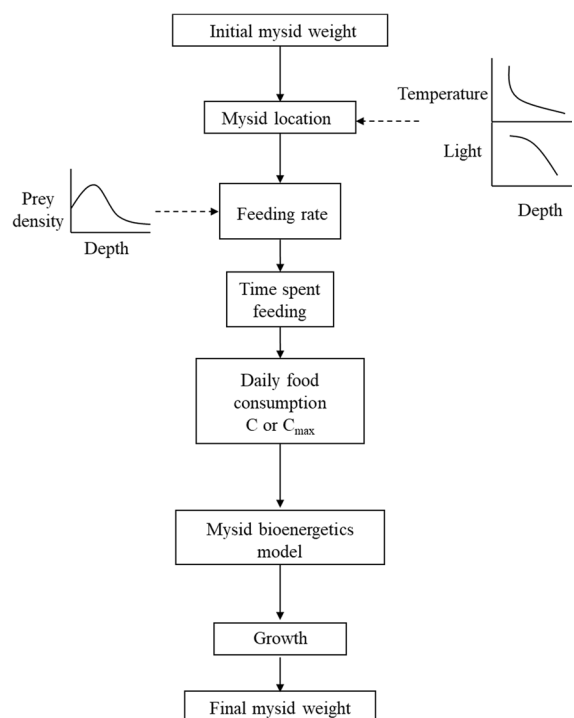


Fig. 1 Combined foraging-bioenergetics model used to estimate daily growth of adult *M. diluviana* ($\geq 15 \text{ mm}$) during new and full moon periods in Lake Pend Oreille, Idaho. Daily food consumption (C or C_{max}) was used as input in a bioenergetics model to estimate daily mysid growth. See text for descriptions of C and C_{max} . Adapted from Bevelhimer & Adams (1993)

Results

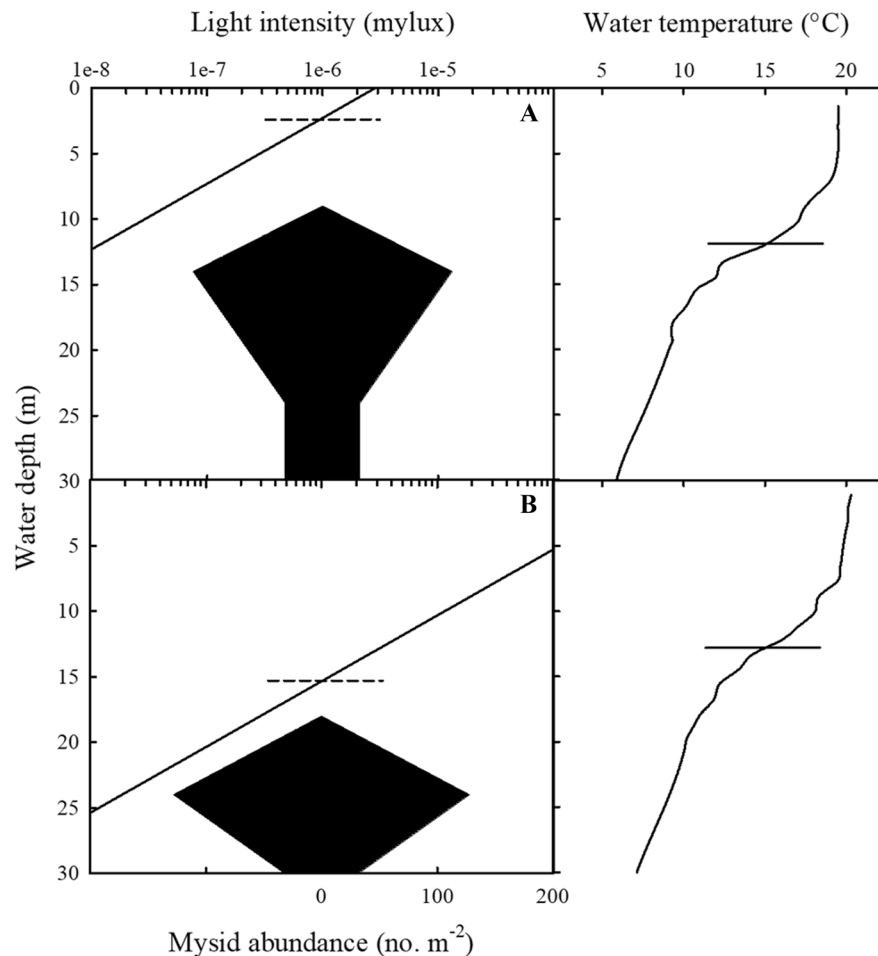
Vertical migration behavior

At 4% moon illuminance on August 16th, mysids ascended at an average rate of 0.8 m min^{-1} and completed their migration by 21:30 h. Adult mysids (mean size = 28.5 mg, TL = 15.8 mm) migrated within 9 m of the water surface where water temperature, rather than light intensity, appeared to limit the upper distribution of *M. diluviana*. Estimated light level on the water surface of Lake Pend Oreille was 2.85×10^{-6} mylux (0.0005 lx). Because of low light conditions, the avoidance threshold of *M. diluviana* (10^{-6} mylux) occurred at a depth of about 2.5 m below the water surface where water temperature exceeded 15°C (Fig. 2). Peak density of mysids (112 m^{-2}) occurred between 9 and 18 m (midpoint ~ 14 m) at a mean

feeding temperature of 11.2°C (Fig. 2). Total density of adult mysids in the upper 30 m averaged $178 \text{ individuals m}^{-2}$ and they began their morning descent around 04:00 h on August 17th, after spending 6.5 h foraging in the metalimnion.

At 97% moon illuminance on August 26th, mysids ascended at a rate of 0.7 m min^{-1} and completed their migration by 21:00 h. Adult mysids (mean weight = 30.5 mg, TL = 16.1 mm) migrated within 18 m of the water surface with a peak density (128 m^{-2}) occurring between 18 and 30 m (midpoint ~ 24 m) at a mean feeding temperature of 8.9°C . Estimated light level on the water surface of Lake Pend Oreille was 1.14×10^{-3} mylux (0.2 lx). In contrast to dark moon conditions, the upper distribution of mysids during the bright moon phase was constrained by light intensity, rather than water temperature (Fig. 2). Light level corresponding to the *M.*

Fig. 2 Depth-specific abundance of adult *M. diluviana* ($\geq 15 \text{ mm}$) during **A** new moon or **B** full moon periods in Lake Pend Oreille, Idaho. Dashed, horizontal lines correspond to the light avoidance threshold of *M. diluviana* (10^{-6} mylux). Solid, horizontal lines correspond to shallow, warm water layers ($\geq 15^\circ\text{C}$) typically avoided by migrating *M. diluviana*



diluviana avoidance threshold (10^{-6} mylux) occurred at a depth of ~ 15 m and corresponded closely to the upper distribution of the mysid layer. Total density in the upper 30 m averaged 168 mysids m^{-2} on August 26th, similar to that observed during the dark moon phase (178 mysids m^{-2}). *M. diluviana* began their descent around 04:00 h on August 27th after spending 7 h foraging in the metalimnion.

M. diluviana consumption and growth

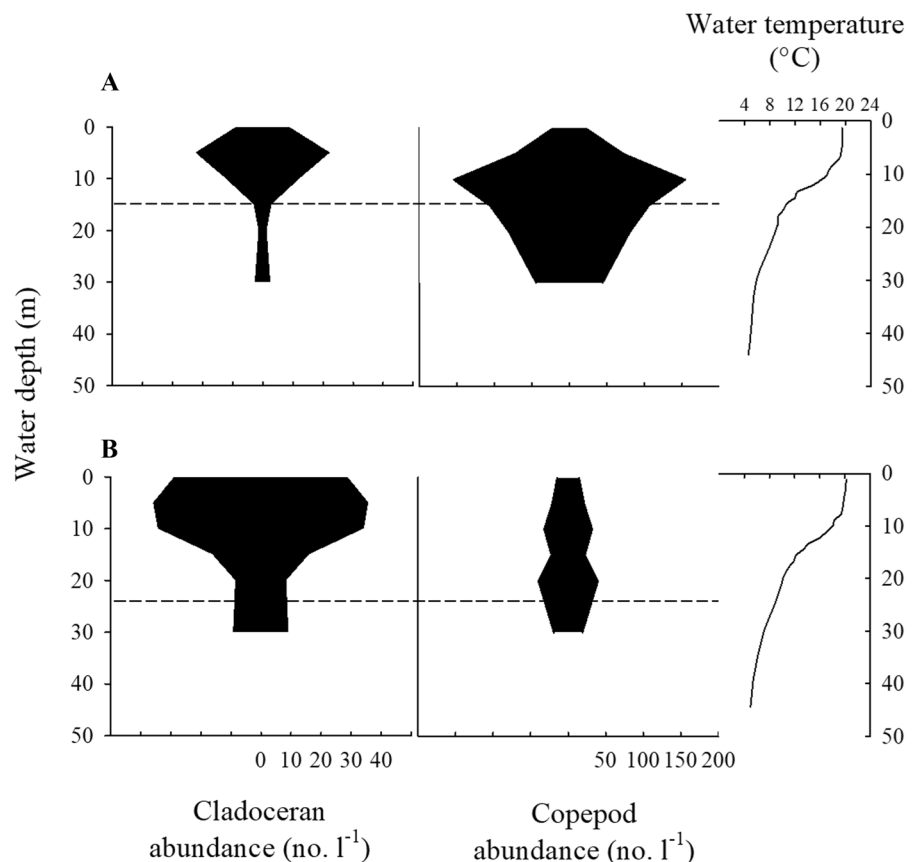
On the night with dark moon conditions, adult copepod abundance at depths corresponding to peak mysid density (15–20 m) averaged 80.4 l^{-1} ($n=6$, $SE=13.1$), and consisted of 54.3% *Diacyclops bicuspidatus* Claus, 1857 and 45.1% *Leptodiaptomus ashlandi* (Marsh, 1893). Copepodid density at 15–20 m averaged 19.2 l^{-1} ($n=6$; $SE=4.7$; Fig. 3). On the evening with bright moon conditions, adult copepod abundance at depths corresponding to peak mysid density (20–30 m) was lower (mean= 9.5 l^{-1} , $n=6$,

$SE=4.7$) than that observed during the dark moon phase and consisted of 61.2% *D. bicuspidatus* and 38% *L. ashlandi*. Copepodid density during the bright moon phase was also lower than that observed during dark moon conditions, averaging 9.6 l^{-1} ($n=6$; $SE=3.5$; Fig. 3).

Mean abundance of cladoceran zooplankton at water depths corresponding to peak mysid density was lower on the night with dark moon conditions (2.0 l^{-1} , $n=6$, $SE=0.8$) compared to bright moon conditions (8.8 l^{-1} , $n=6$, $SE=2.6$; Fig. 3). Moreover, *Daphnia galeata* Sars, 1864 represented a larger proportion of cladoceran abundance (73%) on the evening with bright moonlight compared to dark moon conditions (15%), with *Diaphanosoma birgei* Kořínek, 1981 constituting the remaining 27–85%, respectively.

Greater abundance of Cladocera prey, combined with high clearance rates for these crustaceans and longer foraging time by mysids (+0.5 h) on August 26–27th, resulted in greater energy acquisition during

Fig. 3 Vertical distribution of Cladoceran or Copepod abundance during **A** new moon or **B** full moon periods in Lake Pend Oreille, Idaho. Dashed, horizontal lines correspond to the depth of peak, *M. diluviana* abundance for each period. Corresponding water temperatures are shown in the panel on the right



bright moon conditions (6.1 J day^{-1}) compared to dark moon conditions (4.9 J day^{-1} ; Table 3). Simulated growth derived from bioenergetics modeling revealed that an average, adult *M. diluviana* grew 0.11 mg day^{-1} during dark moon conditions, when their vertical migration was constrained by warm water temperature ($\geq 15^\circ\text{C}$). In contrast, simulated growth rate was greater during the bright moon phase (0.35 mg day^{-1}) corresponding to increased zooplankton consumption and slightly cooler water temperatures experienced by mysids on this night (Table 3).

Simulated migration

On the night with bright moonlight, simulated migration and growth of adult *M. diluviana* was modeled by assuming mysids migrated into the warmer and shallower strata (15 to 20 m) observed during the dark moon phase. In this scenario, average metalimnetic water temperatures experienced by migrating mysids increased from 8.9 to 11.2°C . Under simulated conditions, prey consumption by an average, migrating

adult mysid was estimated at $4.5 \text{ mg prey day}^{-1}$, resulting in a C/C_{max} ratio of 1.2. Because $C/C_{\text{max}} > 1$, we used C_{max} (i.e., maximum feeding rate) as an estimate of daily prey consumption (3.6 mg day^{-1}) as input in the bioenergetics model to simulate daily growth. Daily growth of an average *M. diluviana* based on the simulated migration was 0.61 mg day^{-1} , or about 74% greater than modeled growth based on their observed migration (0.35 mg day^{-1} ; Table 3). In contrast, simulated migration for the dark moon phase resulted in mysids being distributed in deeper, cooler water compared to observed conditions. As a result, *M. diluviana* experienced a 10% weight loss ($-0.95 \text{ mg day}^{-1}$) by *not* migrating into shallower, warmer strata with greater prey densities (Table 3).

Discussion

The vertical distribution of migrating *M. diluviana* is primarily dependent on light intensity and water temperature (Teraguchi et al., 1975; Beeton & Bowers, 1982; Gal et al., 1999; Boscarino et al., 2009a),

Table 3 Migration attributes and depth-specific zooplankton density used to simulate daily feeding and growth of an adult, migrating *M. diluviana* ($\geq 15 \text{ mm}$) in Lake Pend Oreille, Idaho on nights with dark or bright moonlight

| Parameter | Dark moon August 16–17th (4% illuminance) | | Bright moon August 26–27th (97% illuminance) | |
|---|---|-------------|--|------------|
| | Actual | Simulated | Actual | Simulated |
| <i>M. diluviana</i> migration attribute | | | | |
| Nocturnal depth distribution, (m) | 15–20 | 20–30 | 20–30 | 15–20 |
| Mean nocturnal, foraging temperature, ($^\circ\text{C}$) | 11.2 (0.5) | 8.9 | 8.9 (0.4) | 11.2 |
| Mean daily temperature, ($^\circ\text{C}$) | 6.7 (0.7) | 5.8 | 5.8 (0.5) | 6.7 |
| Mean zooplankton density, (l^{-1}) | | | | |
| Copepoda | 99.6 (18) | 62.4 (18.5) | 29.1 (8.3) | 37.7 (7.5) |
| Cladocera | 2.0 (0.8) | 2.1 (0.8) | 8.8 (2.5) | 14.9 (7.6) |
| Estimated <i>M. diluviana</i> feeding rate, (day^{-1}) | | | | |
| No. zooplankton | 103.8 | 66.3 | 63.8 | 95.5 |
| mg zooplankton | 2.1 | 1.41 | 2.7 | 3.6 |
| J zooplankton | 4.9 | 3.33 | 6.1 | 10.3 |
| Estimated <i>M. diluviana</i> growth rate, (mg day^{-1}) | | | | |
| | 0.11 | -0.95 | 0.35 | 0.61 |

Actual migration attributes represent observed values. Simulated migration attributes were used to evaluate the energetic tradeoff experienced by mysids during dark or bright moon conditions. For the Dark moon phase, the Simulated migration attributes were adjusted to match the Actual migration attributes of mysids during the Bright moon phase—when mysids were distributed deeper in the water column. Similarly, for the Bright moon phase, the Simulated migration attributes were adjusted to match the Actual migration attributes during the dark moon phase—when mysids were distributed at shallower water depths. Values in parentheses represent 1 S.E

although consequences of their migration behavior on daily feeding and growth rate have been difficult to quantify. Daily feeding by mysids estimated from clearance rates appeared reasonable (7–9% day⁻¹) and were within the range reported for *M. diluviana* based on laboratory and field studies (7–38% day⁻¹; Cooper & Goldman, 1980; Chipps & Bennett, 2002). Moreover, daily growth predicted by our modeling simulations averaged 0.23 mg day⁻¹ in August (range, 0.11 to 0.35 mg day⁻¹) and was similar to observed growth rate of adult *M. diluviana* (0.20 mg day⁻¹) in Lake Pend Oreille during the same time period (Chipps & Bennett, 2000). Using a combined foraging-bioenergetics modeling approach, we show that during bright moon conditions in August, *M. diluviana* could suffer a daily growth loss of up~70% by remaining at low light levels corresponding closely to reported light avoidance (Teraguchi et al., 1975; Gal et al., 1999; Boscarino et al., 2009a).

Several inferences can be made about *M. diluviana* foraging success related to dark or bright moon conditions. Although foraging during dark moon conditions may reduce predation vulnerability, it does not necessarily result in greater energy gains for *M. diluviana* compared to bright moon conditions. During the dark moon phase, the upper distribution of mysids was physiologically constrained by warm water temperature (> 15°C; Chipps, 1998). But more importantly, preferred prey abundance (i.e., *Daphnia* spp.) was lower during the dark moon phase (mid-August) compared to bright moon conditions (late-August) and this pattern was consistent with seasonal abundance of *D. galeata* observed in Lake Pend Oreille (Rieman & Falter, 1981; Chipps & Bennett, 2000). Had mysids remained in cooler, deeper water similar to conditions observed during a bright moon, they would have experienced an energetic loss (i.e., negative growth). Conversely, during bright moon conditions, *M. diluviana* were behaviorally constrained to deep water because increased light levels limited their upward migration that precluded them from accessing greater prey densities. Thus, the observed distribution of *M. diluviana* during bright moon conditions resulted in an energetic tradeoff where avoiding exposure to greater light intensity came at a cost to daily growth (Lampert, 1993).

In addition to DVM, *M. diluviana* exhibits other life-history traits consistent with predator avoidance behavior. *M. diluviana* avoid waters that contain

kairomones of fish predators such as Alewife *Alosa pseudoharengus* (Wilson, 1811) and the presence of these fish has been linked to low mysid abundance (Boscarino et al., 2007, 2010b). As in other deep lakes, *M. diluviana* in Lake Pend Oreille spend a considerable portion of the day on the bottom of the lake at depths > 150 m (Chipps & Bennett, 2000). At these depths, cold water temperature (4°C) and less favorable foraging conditions create tradeoffs to avoiding predators that include (i) low fecundity, (ii) long embryonic development time (e.g., 200–280 days; Mauchline, 1980), and (iii) long generation time (1 to 4 years; Morgan, 1980; Chess & Stanford, 1998). Although the relatively large size of *M. diluviana* (~20 mm) make them more vulnerable to fish predation, large body size may also serve as an adaptation to low food production given that metabolic efficiency is positively related to body size among a variety of taxa (Kleiber, 1947; Hatton et al., 2019). Larger body size may confer other benefits that include a greater ability to withstand starvation, enhanced mobility, and increased access to a variety of benthic (detritus) and pelagic (phytoplankton and zooplankton) food sources (Spight, 1976; Rex et al., 1999).

While predator avoidance is the most widely accepted hypothesis concerning the regulation of DVM in zooplankton (Zaret & Suffern, 1976; Gliwicz, 1986), other hypotheses have been proposed to explain this behavior (Enright, 1977). The bioenergetics efficiency hypothesis (McLaren, 1963) proposes an energetic advantage to DVM, where a “hunt warm, rest cool” strategy confers an energetic advantage to animals undergoing DVM (Sims et al., 2006). The bioenergetics efficiency hypothesis is based on the premise that feeding in warm, prey rich strata coupled with migrations into deeper, cooler water, results in a net energetic and(or) reproductive gain. For vertically migrating fish like Kokanee Salmon, this hypothesis has been supported (Bevelhimer & Adams, 1993) although other ultimate causes of DVM among salmon have been proposed (Johnston, 1990; Mehner, 2012). The bioenergetics efficiency hypothesis has generally not been supported as an ultimate factor driving DVM behavior among aquatic invertebrates (Swift, 1976) and appears to be more suited to animals that do not undergo extensive DVMs and(or), do not spend considerable time in sub-optimal water temperatures (Lampert, 1989).

Bright moonlight is known to disrupt the migratory behavior of *M. diluviana*, potentially inhibiting their nighttime feeding rates (Beeton & Bowers, 1982). To reduce cannibalism by adult *M. diluviana*, immature mysids complete their nighttime ascent to surface waters earlier than adults and begin their morning descent later (Beeton & Bowers, 1982; Quirt & Lasenby, 2002). Related work with *Euphausia pacifica* Hansen, 1911 has shown that size-dependent differences in DVM can be explained by increased energy gain and vulnerability to predators (De Robertis, 2002). Smaller *E. pacifica* ascend/descend about 35 min earlier/later than adults resulting in increased foraging time and energy gain (De Robertis, 2002). Similarly, as a relatively large zooplankter, *M. diluviana* is more visible to planktivorous fishes than smaller-bodied zooplankton (Brooks & Dodson, 1965; Zaret, 1980; Beeton & Bowers, 1982). In the laboratory, immature *M. diluviana* tolerated greater light levels than larger individuals, enabling them to occupy shallower surface waters compared to adults (Boscarino et al., 2010b). The small size and reduced pigmentation of immature mysids may reduce their vulnerability to visually feeding fishes compared to larger individuals (Quirt & Lasenby, 2002), consistent with the predator avoidance hypothesis (Fiksen & Giske, 1995).

In the currency of predator avoidance, DVM behavior can be expressed as minimizing the trade-off (μ/g) between predation mortality (μ) and energy gain (g); in practical terms, this means that *M. diluviana* ascend and descend to/from surface waters and choose foraging habitats that minimize μ/g (De Robertis, 2002). On nights with bright moonlight, the close association between the light avoidance threshold of *M. diluviana* (10^{-6} mylux) and their upper distribution revealed that water temperature and prey density had little influence on the extent of their upward migration. Thus, the perceived risk of light-dependent mortality outweighed the benefit of migrating into warmer strata with greater prey density.

Our study was limited to observations of DVM behavior by adult *M. diluviana* during late summer conditions when Lake Pend Oreille was thermally stratified. Although the duration of thermal stratification is relatively short in Lake Pend Oreille (e.g., late July through September), it is characterized by warm, epilimnetic water temperatures (18–20°C),

greater Cladocera abundance, and greater *M. diluviana* growth compared to non-stratified and isothermal conditions in the lake (Chippis & Bennett, 2000). Late summer for adult mysids is also an important time in their ontogeny. *M. diluviana* attain sexual maturity during August–September of their second growing season, when the growth rate of females exceeds that of males (Morgan, 1985; Chippis & Bennett, 2000). Thus, balancing energy acquisition against asset protection (e.g., eggs; Clark, 1994) may become increasingly important for *M. diluviana* in late summer, particularly if predation risk is high.

Kokanee, Rainbow Trout, and Cutthroat Trout are important pelagic predators of *M. diluviana* in Lake Pend Oreille. Bioenergetics modeling has shown that monthly food consumption by the Kokanee population was 1.2 to 2.7 times greater in late summer (August–September) compared to other months (Chippis & Bennett, 2000). Although young Rainbow Trout (<450 mm) are less abundant (~ 0.1 kg ha $^{-1}$; Vidergar, 2000) than Kokanee (~ 16 kg ha $^{-1}$; Chippis & Bennett, 2000), diet analysis showed that *M. diluviana* was the second most important prey item for Rainbow Trout, representing 35% of their diet by weight (Vidergar, 2000). Moreover, the percent of empty stomachs among Rainbow Trout was lowest in August and September (0 to 6%) compared to other months (13 to 45%; Vidergar, 2000), implying that feeding activity and potential predation on mysids was greatest during late summer. Thus, the trade-off between avoiding predators or maximizing daily energy acquisition may be greater for adult *M. diluviana* during late summer conditions when preferred prey are most abundant. But avoiding predators at the expense of greater growth may have implications beyond just individual survival. From a population perspective, short-term growth loss for an adult *M. diluviana* may be less important than the opportunity to reproduce at times when DVM behavior may be influenced by asset protection and maximizing long-term population growth (Clark, 1994).

Although not examined in our study, partial DVM by *M. diluviana* is an underappreciated aspect of their vertical migration behavior (Euclide et al., 2017; Stockwell et al., 2020). In Lake Champlain, Vermont, USA the nighttime proportion of gravid *M. diluviana* was greater in benthic (non-migrating) than in pelagic (migrating) habitat during November when thermal stratification was absent (Euclide

et al., 2017). Body condition among non-gravid individuals revealed that lipid content was 9–18% greater for mysids collected from benthic compared to pelagic habitats, leading the authors to postulate that energy reserves may play a role in determining the frequency at which individual *M. diluviana* undergo DVM. Comparisons of gravid *M. diluviana* showed that they were more abundant in nighttime benthic samples than pelagic samples supporting the asset protection principle of anti-predator behavior (Clark, 1994; Euclide et al., 2017).

Viewed in the context of migratory behavior, proximate factors associated with pelagic distribution of migrating individuals (e.g., water temperature, light availability) combined with those associated with benthic distribution of non-migrating individuals (e.g., hunger level, reproductive status) may convey complimentary benefits to *M. diluviana* by contributing to both reduced predation mortality and increased growth conversion (e.g., “hunt warm; rest cool”, Sims et al., 2006). Future efforts aimed at documenting the combined benefits of migrating and non-migrating behaviors among zooplankton that exhibit vertical migration will contribute to a better understanding of one of the world’s most significant, synchronized animal behaviors.

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Data availability The datasets analyzed for the study are available from the corresponding author on reasonable request.

Code availability Not applicable.

Declarations

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